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DYNAMICS AND FUNCTIONING OF *RHODODENDRON FERRUGINEUM* SUBALPINE HEATHLANDS (NORTHERN ALPS, FRANCE)

Mineral nitrogen availability in the context of global climate change

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INTRODUCTION

It is now known and accepted that global climatic change could modify the dynamics and the functioning of mountain ecosystems. Indeed, at high altitudes, climate is considered the major limiting factor for many plants. The pathways by which this change in climate could act upon plant communities, both directly or indirectly, are numerous. Example of this are the effects of increased levels of atmospheric CO_2 on photosynthesis, and the effects of temperature increase on the metabolism or the absorption of nutrients by the plants, etc. The manner in which climatic change could act by indirect pathways is not as yet very well studied. However it has been shown that temperature and humidity may affect biological cycles (Blackman, 1936; Dadykin, 1958; Bonneau, 1980; Tavant, 1986; Roze, 1986)—mainly the nitrogen cycle. The quantity of available nitrogen acts on plant populations by means of their biomass, productivity, reproduction, and intra-specific competition (Aarssen and Burton, 1990; Bonneau, 1980; Le Tacon and Millier, 1970; Le Tacon, 1972; Vermeer and Berendse, 1983; Roze, 1986; Hull and Hooney, 1990). In turn, soil temperature and humidity can affect nitrogen availibility by either of two pathways.

(1) Direct pathway—Blackman (1936) and Dadykin (1958) have found nitrogen uptake by plants to be inhibited by low spring soil temperature. Conversely, high spring soil temperature can allow a better uptake. (2) Indirect pathway—in the moist, cold and acid soils (that is to say high-altitude soils) such processes as ammonification and above all nitrification are reduced. As a result, the quantity of mineral nitrogen (which is the form mostly used by plants) is reduced. In addition, this mineral nitrogen occurs principally as $N\text{-}NH_4^+$ ions with only negligible amounts of nitrates being present (Bonneau, 1980; Tavant, 1986).

As a result of global climatic change, the soil temperature will increase the amount of mineral nitrogen, and therefore the balance of the $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ ions will be modified. Thus, interactions between particular plant communities could be affected. Indeed, the ability of plants to absorb $N\text{-}NH_4^+$ or $N\text{-}NO_3^-$ varies. It has been observed that woody plants, such as spruce, are able to use nitrogen in both $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ forms (Hoffmann, 1966; Hoffmann and Fiedler, 1966), while grasses are only able to use $N\text{-}NO_3^-$ ions. More recently though, it has been observed that if $N\text{-}NO_3^-$ ions are used more by woody plants, it is only in the case where its soil concentration is greater than the concentration of the $N\text{-}NH_4^+$ (Boxman and Roelofs, 1988; Scheromm and Plassard, 1988). All these investigations show that mineral nitrogen forms clearly influence the developmental processes of high-altitude plant communities.

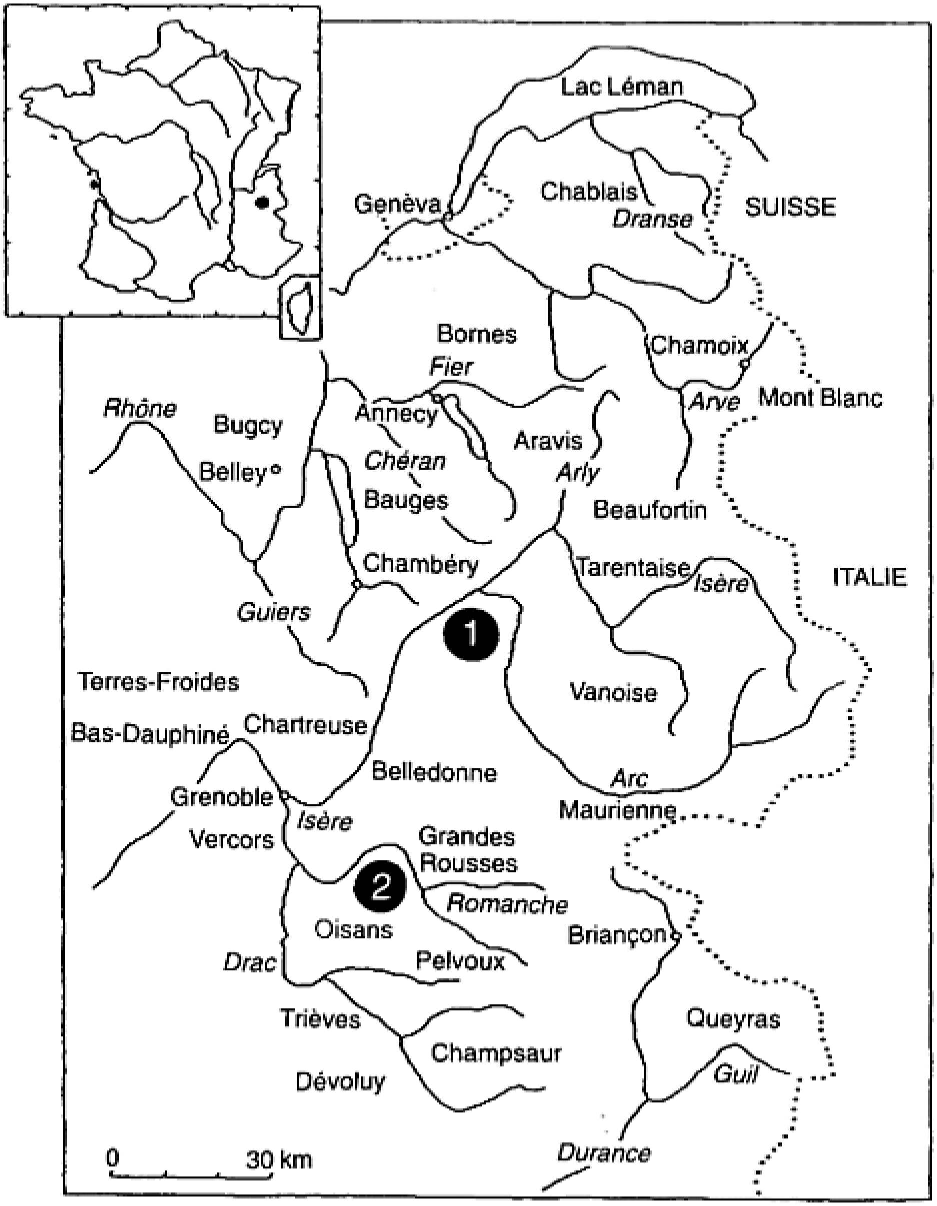

Figure 15.1 The study sites in the northern Alps (France): 1—Belledonne; 2—Taillefer.

In this paper, we show how soil temperature acts on the amounts of both N-NH_4^+ and N-NO_3^- present in the soil and how that in turn could influence the productivity and the dynamics of the *Rhododendron ferrugineum* populations of two similar successions; from meadow to closed heathland in the subalpine level.

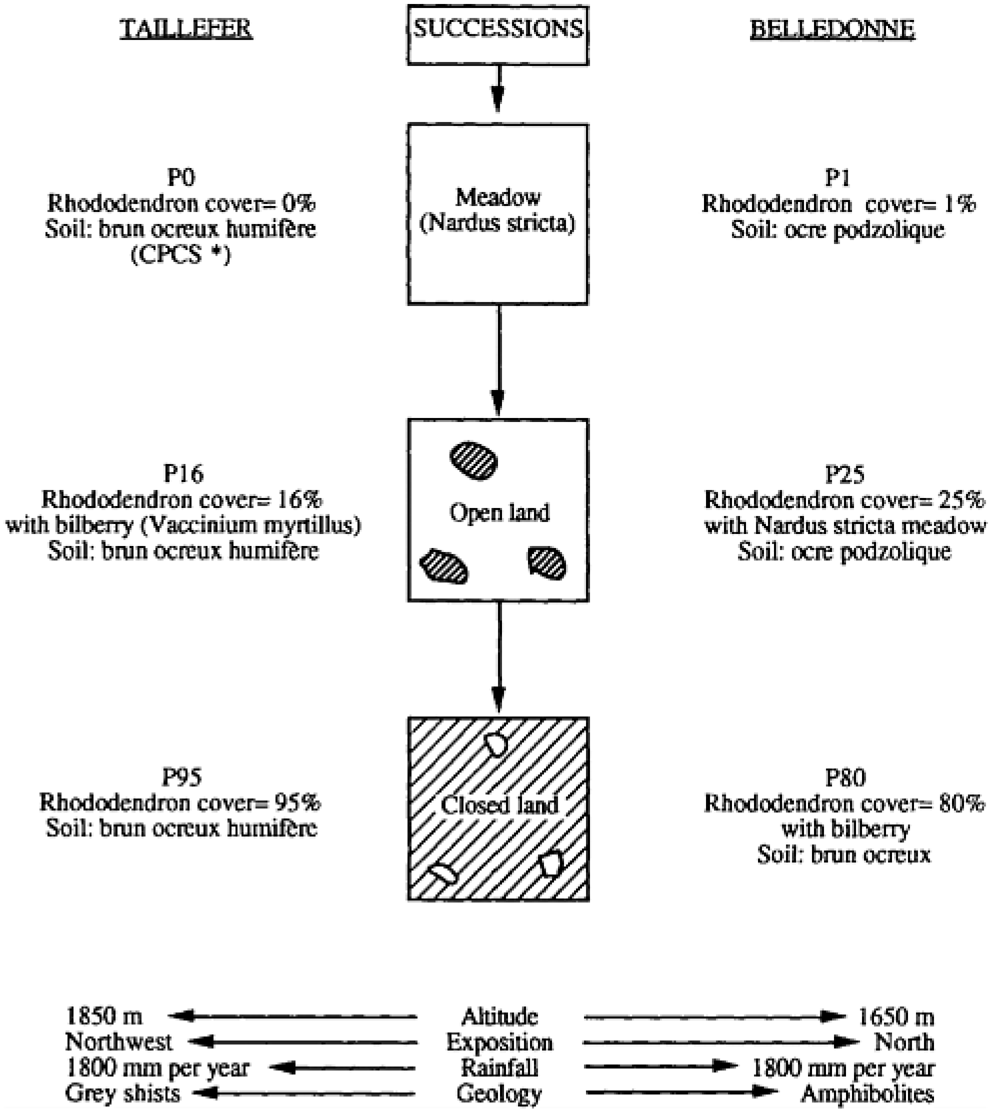

Figure 15.2 Description of sites and the successions of vegetation.

SPECIES STUDIED AND STUDY SITE

Rhododendron ferruginenm is an evergreen shrub (Ericaceous) with a height of 70 cm, which grows at the subalpine level from about 1,600 to 2,200 m. In the northwestern Alps, it forms very large heathlands on the north and northwest facing slopes.

The study sites are ‘Collet d’Allevard’ (45° 25'N, 6° 10'E) in the Belledonne massif, and ‘Côte des Salières’ (45° 4'N, 5° 58'E) in the Taillefer massif (Figure 15.1), in France.

At each study site, we studied the succession from meadow to closed heathland, the environmental features of which are summarized in Figure 15.2.

METHODS

The demography of the *Rhododendron* populations was carried out by studying the age of all the stands within a 100 m^2 area in six different plots both at Belledonne and at Taillefer. The age of stands is given by counting the annual rings on the widest stem of each individual.

For the productivity of shoots (1992), the results were obtained from collecting material in twenty 6.25 dm^2 squares along three separate transects in each plot of the two sites. The space between two squares was 2 m.

In order to calculate the productivity of the shoots, the material from each square was dried at 105°C and then weighed. The data shown in Table 15.1 are the averages of twenty samples. For all the averages, the confidence interval was calculated with an error risk of 5 per cent.

The soil mineral nitrogen content was studied as follows: the amounts of $N\text{-}NO_3^-$ and $N\text{-}NH_4^+$ were measured both in undisturbed humus and in humus samples which had been incubated *in situ* for one month. These measures were repeated each month for three months during the plant's growing season. The samples were incubated in order to prevent leaching by rainfall and uptake by the plants of the mineral nitrogen. The data concerning the undisturbed humus was obtained from ten samples of the upper soil level (5 cm), while for incubated humus the data was obtained from four incubations. For the incubation of the humus, we used a method similar to one proposed by Roze (1986). $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ were extracted according to the method of Wheatley *et al.* (1989). The amount of $N\text{-}NH4_+$ was measured by the blue indophenol method (Nelson and Dorich, 1983) and the amount of $N\text{-}NO_3^-$ was measured by High Performance Liquid Chromatography (HPLC, Dionex 4500 i).

Table 15.1 Current-year shoot productivity (g of dry weight /m^2) for different *Rhododendron* populations (p=0.05)

Plots	*P 25*	*P 80*	*P 16*	*P 95*
Shoots (gDW/m^2)	329.1 ±28.83	417.21 ±46.52	229.56 ± 34.99	254.09 ± 34.53
Fruit (%)	4.6	2.75	6	2
Leaves and Twigs	95.5	97.25	94	98
		Taillefer		*Belledonne*
Meadow Productivity (g DW/m^2)		580		100

Soil temperature was measured every week during the growing season with hygrometic probes Wescor POT-55 connectable to a Wescor HR-33T micro voltmeter buried in the soil at depths of 10 and 25 cm.

RESULTS

The dynamics of the *Rhododendron* populations

A *Rhododendron ferrugineum* heathland, which is not in competition with other offensive woody species, needs 150 years to extend throughout a meadow area and to occupy 80–90 per cent of it (Pornon, 1993).

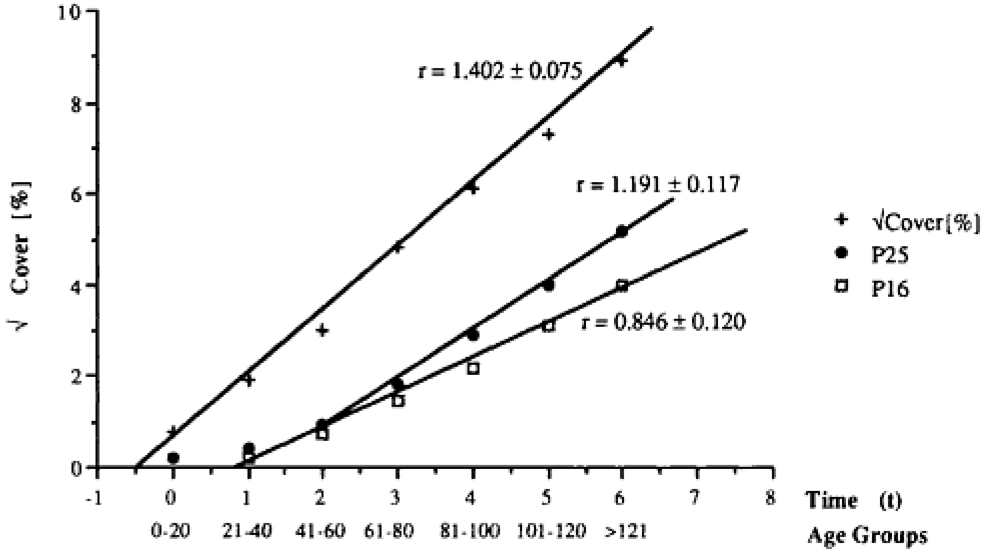

Figure 15.3 Population growth rate for Belledonne (P 80, P 25) and for Taillefer (P 16).

In order to compare the colonization efficiency of *Rhododendron,* we calculated the population growth rate (Figure 15.3).

In P 80, the growth rate is constant with time and the gradient reaches 1.4. In almost closed heathlands, the installation of new individuals is possible and the colonization is continued by vegetative means.

Early in the colonization in P 25, the growth rate is smaller than that in P 80 because cattle probably have been a controlling influence on the youngest stands.

At Taillefer, in P 16, the growth rate is smaller than in P 80 and P 25 because the environmental factors are not so well suited to the *Rhododendron*.

Current-year shoot productivity

Table 15.1 shows shoot productivity for 1992. It may be observed that the productivity shows the same pattern as the dynamics of *Rhododendron;* the plots in which the dynamics are more efficient are the ones in which the productivity is the greatest. In P 80, the shoot productivity was 417.21 g DW/m^2 for the year 1992 and for P 25 and P 16, the shoot productivity was 329 g DW/m^2 and 229 g DW/m^2 respectively.

To summarize: the three following factors influence the development and functioning of the heathlands at the different study sites:

- The degree of population cover: in closed heathlands the productivity is higher than in open heathlands.
- The grazing pressure: in P 80 the slope is steeper. Consequently it was not easily accessible to animals. In the past, therefore, the conditions for the development of the *Rhododendron* were more favourable.
- The pedological characteristics: at Belledonne the pedological characteristics are much more suited to the *Rhododendron* than at Taillefer.

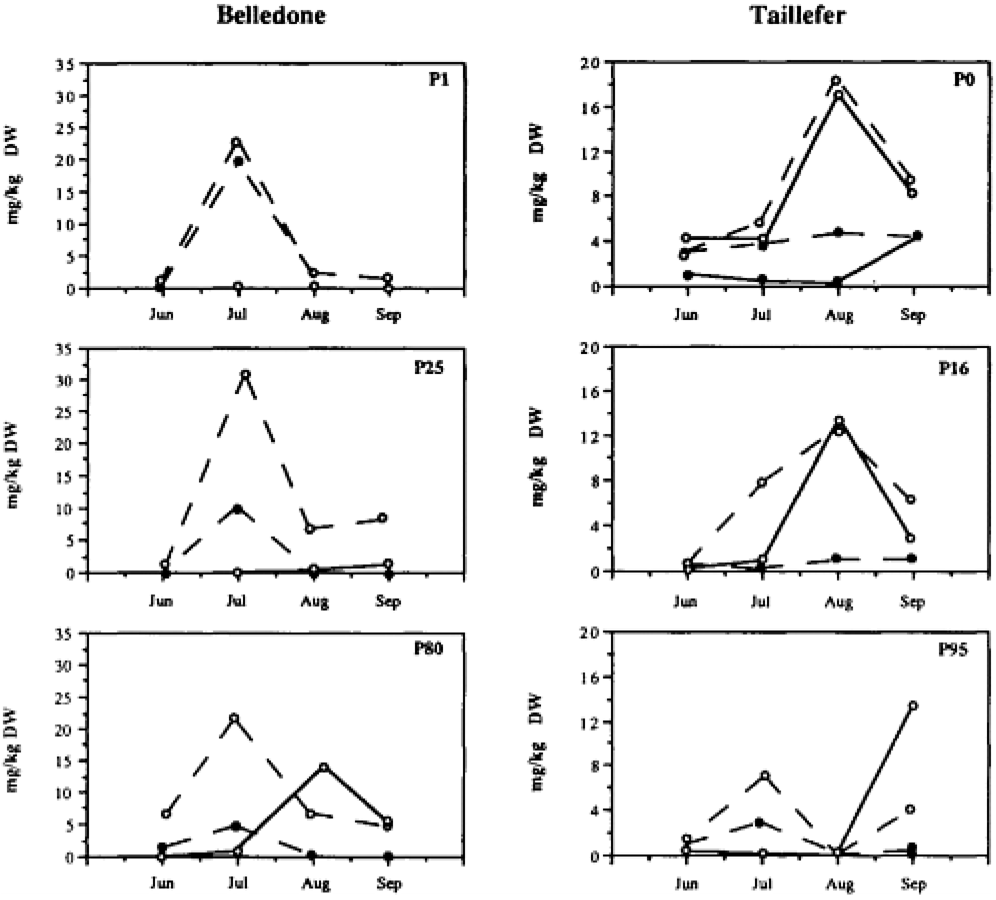

Figure 15.4 Nitrogen concentration (dashed line—as N-NH_4^+; continuous line—as N-NO_3^-) in humus incubation 'in situ' during one month (open circles); in undisturbed humus (closed circles). All samples taken on the 12th of each month.

The soil mineral nitrogen

The highest mineral nitrogen content of the incubated samples was found at Belledonne (Figure 15.4) during the period June-July. It can also be observed that nitrogen is mostly in the form of N-NH4+. Open heathlands produce the greatest amounts of this element (30 mg/kg DW of soil) whereas closed heathlands produce the smallest (20 mg/kg DW of soil) conversely to its higher biomass production.

In the undisturbed humus layer of the meadow, the concentration of N-NH_4^+ (20 mg/kg DW) was found to be similar to that of the incubated humus (24 mg/kg DW). These results indicate that for this period at Belledonne, the meadow plants either cannot at all, or can but only in very small quantities, use N-NH_4^+ ions as a nutrient. On the contrary, in the open and closed heathlands, the results show that *Rhododendron* can readily use this nutrient element. The concentration of N-NH_4^+ in the undisturbed humus of the open and closed heathlands (9 and 4 mg/kg DW of soil respectively) were found to be very different to that of the incubated humus (31 and 21 mg/kg DW of soil). There is a loss of N-NH_4^+ in the meadow soils during July-

August which is probably caused by the element being taken up by bacterial biomass during this period. Indeed, in acid soils N-NH_4^+ is not transformed into NH_3 gas (Roze, 1986) and, as is well known, it is in the N-NH_4^+ form that the nitrogen is absorbed by the bacterial biomass in the case where both N-NH_4^+ and N-NO_3^- coexist. This 'reorganization' of N-NH_4^+ is likely to occur in the soils of *Rhododendron* heathlands but its effects are not evident. However, there is probably strong competition between the bacteria and Ericaceous plants for this nitrogen nutrient.

The results also show that nitrates remained at a constantly low level (except for the July-August period in closed heathland) in both the undisturbed humus and the incubated humus (<4 mg/kg DW). Soil nitrate concentration is dependent on spring nitrification which is in turn dependent on the soil spring temperatures. Therefore, if the temperatures are too low, they prevent nitrification and this results in a too low soil nitrate concentration.

The total amounts of mineral nitrogen measured for Taillefer and Belledonne (Figure 15.4) were similar (30 mg/kg DW of soil), and at both sites the closed heathlands had the lowest available nitrogen.

At Taillefer however, there were differences in the functioning of the soil: (i) the peak of mineralization (July-August period) was late and occurred at the end of the *Rhododendron* vegetative season; and (ii) in the meadow and open heathland, the nitrification was greater by a factor of 50 than for meadow and open heathland at Belledonne as soil N-NO_3^- concentration was clearly higher.

Soil temperature and nitrogen mineralization

Figure 15.5 shows the soil temperature during the growing season of 1991 and 1992 for the plots at Belledonne.

It can be seen that the underground temperature for both 1991 and 1992 is lower for closed heathlands than for meadows and such is the trend for nitrogen mineralization. In all the plots, during the second part of plant growth (August), the temperature of the soil was lower by 3 or 4°C in 1992 than in 1991.

It can be seen (Figure 15.6) that in 1992 high N-NH_4^+ concentration corresponds to a low nitrate concentration. On the contrary, during 1991, due to an increase in soil temperature, there was a low N-NH_4^+ concentration and a high nitrate concentration.

These results indicate that at high altitudes, the soil temperature strongly acts on nitrification.

DISCUSSION

Mineral nitrogen and the biology of the *Rhododendron* population

Much research has demonstrated the interactions between the availability of nitrogen and the development of plant populations. The ecosystems at high altitudes, when compared with ecosystems at low altitudes (Brittany heathlands, Roze, 1986) have a much lower soil nitrogen concentration by a factor of between two and six according to the plant communities (Bonneau, 1980).

Some researchers (Bonneau, 1980; Tavant, 1986) have indicated that in mountain milieus, nitrogen is mainly in the form of N-NH_4^+ ions. Our own results for 1992 showed that in reality, however, the situation is more complicated.

At Taillefer, mineral nitrogen exists both as N-NH_4^+ and N-NO_3^- in meadows and in closed heathlands, while it is only present as N-NH_4^+ at Belledonne. During 1992, the soil humidity and temperature were not significantly different between the two sites and therefore do not explain the above differences between

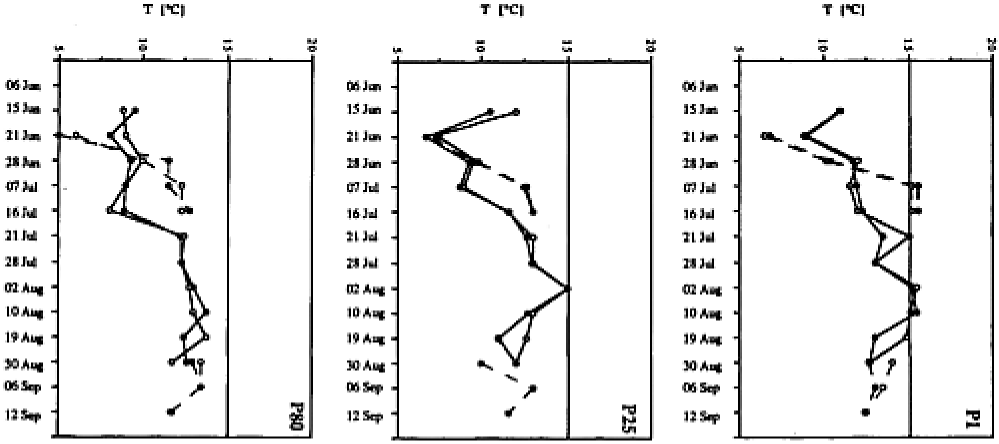

Figure 15.5 Soil temperature for Belledonne. Dashed line—year 1991; continuous line—year 1992; open circles—10 cm depth; closed circles—25 cm depth.

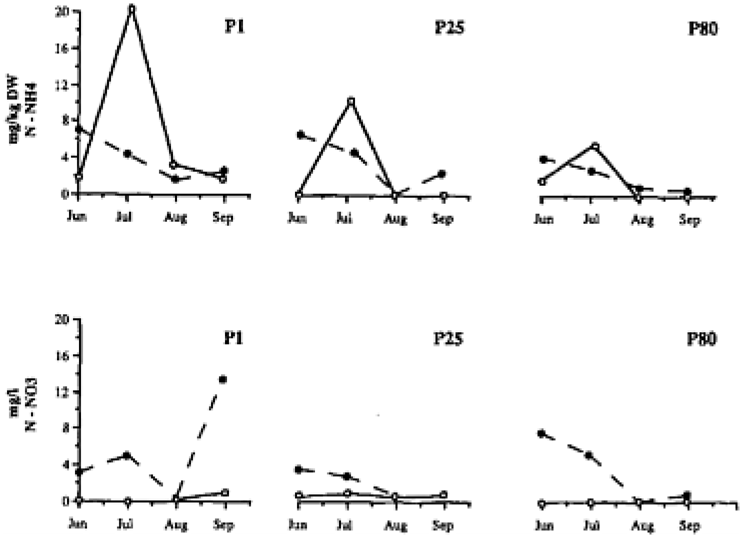

Figure 15.6 Nitrogen concentration as N-NO_3^- and as N-NH_4^+ in soils of the Belledonne. All samples taken on the 12th of each month. Closed circles—year 1991; open circles—year 1992 (p=0.05).

Taillefer and Belledonne. On the contrary, the soil's pH (H_2O) is clearly higher at Taillefer (from 4.7 to 5.5 according to the soil level and the plots) than at Belledonne (from 3.8 to 4.2). pH is often noted as being an influential factor acting on mineralization and above all on nitrification (Le Tacon, 1972; Roze, 1986; Salsac *et al.,* 1987).

Soil temperature is an another influencing parameter. In the case when spring soil temperatures are higher (as for 1991 compared to 1992), even in acid soils (Belledonne), nitrification occurs, so nitrate concentration therefore increases.

These variations of different mineral nitrogen forms are very important because:

(1) The ability of the plant to absorb N-NH_4^+ and N-NO_3^- is different. For Gramineous plants, N-NO_3^- is generally the main nutrient (Salsac *et al.,* 1987) and the environmental factor most limiting to growth of annual grasses is the availability of nitrate nitrogen (Hull and Muller, 1977; Jenny *et al.,* 1980). On the contrary, woody plants are able to absorb both N-NH_4^+ and N-NO_3^- as nutrients (Boxman and Roelofs, 1988; Scheromm and Plassard, 1988; Hoffmann, 1966; Hoffmann and Fiedler, 1966). On the other hand, Le Tacon (1972) noted that the growth of Ericaceous plants is better on soils with N-NH_4^+ compared to soils with N-NO_3^-. Our own results illustrate in detail these two different pathways of plant nutrition. In comparison with Belledonne, where mineral nitrogen was essentially as N-NH_4^+, the productivity of the Taillefer's meadow was greater as mineral nitrogen was equally distributed as N-NO_3^- and as N-NH_4^+. Taillefer's heathlands had smaller productivities than those at Belledonne, which is likely as N-NH_4^+, being the favoured nutrient for *Rhododendron,* was present in a smaller concentration. The lower productivity of Taillefer's heathlands could not be explained only by the low levels of N-NH_4^+ but also by the possible toxicity of N-NO_3^-

(2) The stability of N-NH_4^+ and N-NO_3^- in the soil is different. N-NH_4^+ constitutes a relatively stable pool and indeed in acid soil its leaching by rainfull, 'reversion' in clay, and disappearance as NH_3^+ gas are very limited, while N-NO_3^- is able to disappear by leaching and the 'denitrification' pathway.

Global climatic change and ecosystem functioning

It is evident that with global climatic change, as the soil temperature increases, the balance between the two mineral nitrogen ions will be modified. A pattern may be proposed such that soil temperature could act on the nitrogen flux and interact between particular mixed plant communities (Figure 15.7). With low spring temperatures, mineral nitrogen is essentially as N-NH4$^+$ and consequently there is competition between the Ericaceous and the soil bacteria and there is little nitrate available for the meadow grasses. If soil temperature increases about 2–4°C during the growing season, N-NH_4^+ concentration decreases and N-NO_3^- concentration increases. N-NO_3^- is mainly used by grasses, but there exists a strong competition between Ericaceous, grasses and soil bacteria. Where this occurs a lower productivity of the heathlands also takes place.

The division of nutrients between different species is a probable explanation for why the closed heathlands, in which *Rhododendron* is almost the single species, are more productive than open heathlands in which *Rhododendron* coexists with many other species.

Another effect of the soil temperature increase is that mineralization occurs earlier during the growing season and therefore so does the increase in the availability of mineral nitrogen. This effect particularly concerns sites such as Taillefer where the peak of mineralization occurs at the end of the shoot growth period.

As the N-$N0_3^-$ pool is unstable, the increase in temperature could cause a considerable loss of this element by leaching and denitrification.

CONCLUSION

In a high-altitude environment, climatic conditions are critical to plant communities. Slight fluctuations in temperature and humidity over a long-term period can largely affect the functioning of mountain ecosystems. Our results for the years 1991 and 1992 show the effects of temperature on the nitrogen cycle, nitrogen being a major plant nutrient. With high spring temperatures, the N-NO_3^- soil concentration increases while the concentration of N-NH_4^+ decreases. It is expected that this situation would lead to a

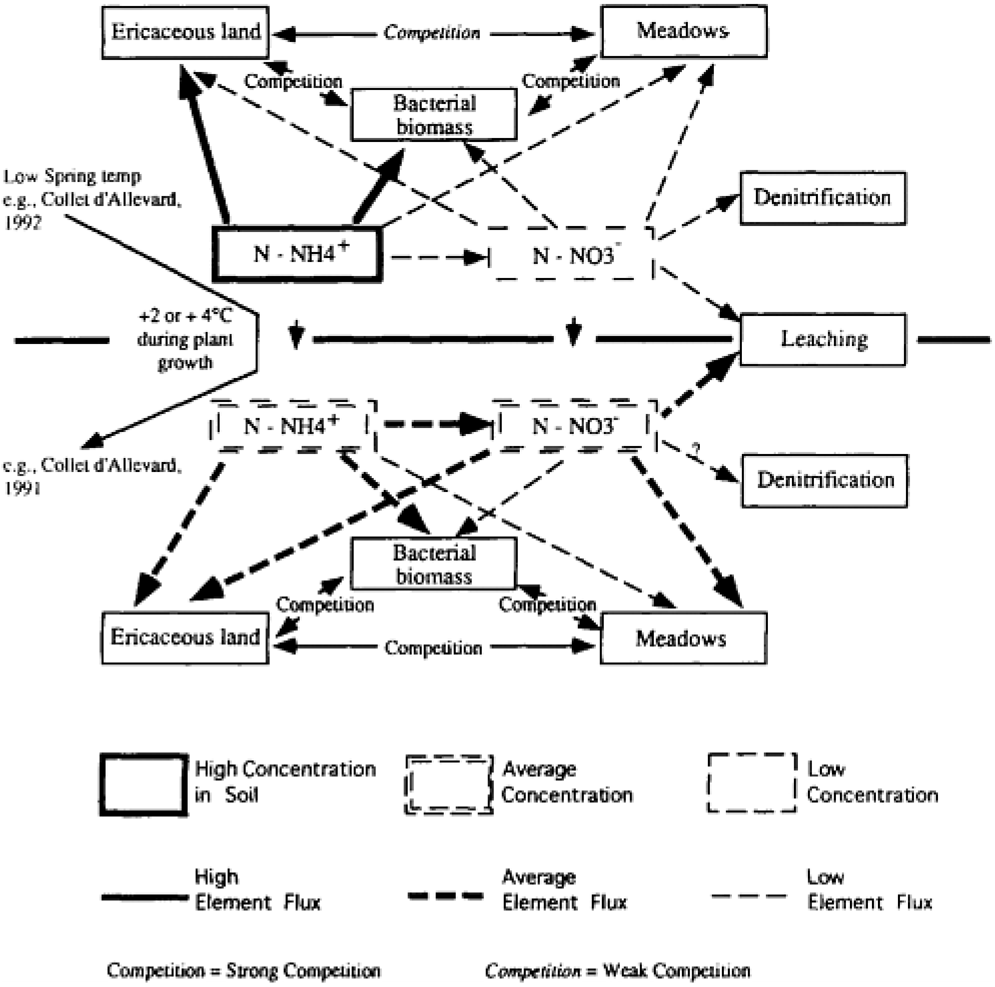

Figure 15.7 Action of soil temperature on available nitrogen flux for different plant populations.

strong competition for nitrogen between the Ericaceous and other plant species, particularly because there is also considerable loss by leaching and denitrification. This is an example of how climatic change could affect the productivity and dynamics of a heathland.

This suggested course of events does not apply to N-flux as it is thought that, with the help of mycorrhizae, *Rhododendron* is able to use organic nitrogen as is seen with *Calluna vulgaris* (Pearson, 1971; Pearson and Read, 1973a and b, 1975; Stribley and Read, 1974a and b). In this case, there is no competition.

The difficulty involved in deducing the long-term effects of climatic change on mountain ecosystems is having only short-term analysis methods at our disposal. In order fully to understand the consequences of global climatic change, long-term studies would be necessary.

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